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An Ecological Study of the Forest Tent Caterpillar, *Malacosoma disstria* Hbn., in Northern Minnesota

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CONTENTS

	Page
Introduction	3
Historical discussion	4
General historical review	4
Outbreaks in Minnesota	7
Bionomics	9
Life history in Minnesota	9
The effect of temperature on larval development	12
The quantity of food eaten	13
Measurements of frass production	15
Host tree preference and food favorable for young larvae	17
The effects of starvation during the last instar	19
Population measurements	20
Cocoon sampling	20
Egg sampling	22
Sampling of larvae and adults	23
Population surveys	24
Egg survey records	24
Predicting the probable degree of defoliation	29
Cocoon survey results	32
Natural control of *Malacosoma disstria*	34
Mortality during the egg stage	34
Mortality among feeding larvae	38
Mortality of prepupae and pupae in the cocoon	39
Adult mortality	43
An evaluation of mortality factors	43
The cyclic behavior of populations of *Malacosoma disstria*	48
Summary and conclusions	52
Literature cited	54

An Ecological Study of the Forest Tent Caterpillar, *Malacosoma disstria* Hbn., in Northern Minnesota[1]

A. C. Hodson[2]

INTRODUCTION

DURING EARLY June of 1935 hordes of caterpillars seemed to appear from nowhere in aspen forests near Ely, Minnesota. These caterpillars defoliated large stands of aspen and caused considerable annoyance to the local residents and thousands of summer tourists who found them everywhere in the woods and even in their cabins. This plague was the result of an outbreak of the forest tent caterpillar, *Malacosoma disstria* Hbn., which is periodically a common pest of deciduous trees in many parts of the United States and Canada. The outbreak began in Minnesota in 1933 and continued with an increasing intensity until the summer of 1938. During this time thousands of acres of broadleaf trees were completely defoliated. In some areas the defoliation continued for four or five consecutive years severely injuring many trees and killing others. General surveys have shown from 20 to 80 per cent of the trees dead, the degree of damage depending upon the site, number of complete defoliations, and age of the trees. In some cases elimination of aspen has released conifers and may be considered a beneficial, natural thinning.

In spite of extensive literature on the forest tent caterpillar and evidence of somewhat regular, periodic outbreaks, there have

[1] Assistance in the preparation of these materials was furnished by the personnel of Work Projects Administration Official Project No. 165-1-71-124, Sponsor, University of Minnesota.

[2] The author is greatly indebted to a number of individuals who have contributed their assistance generously. Among these are Roger Anderson, Rodney Dodge, and Philip Schroeder who worked as field assistants. Professor A. G. Ruggles offered personal observations and considerable administrative help. Rangers in the State and Federal Forest Services were authorized to aid the author in many ways and they conducted most of the egg surveys.

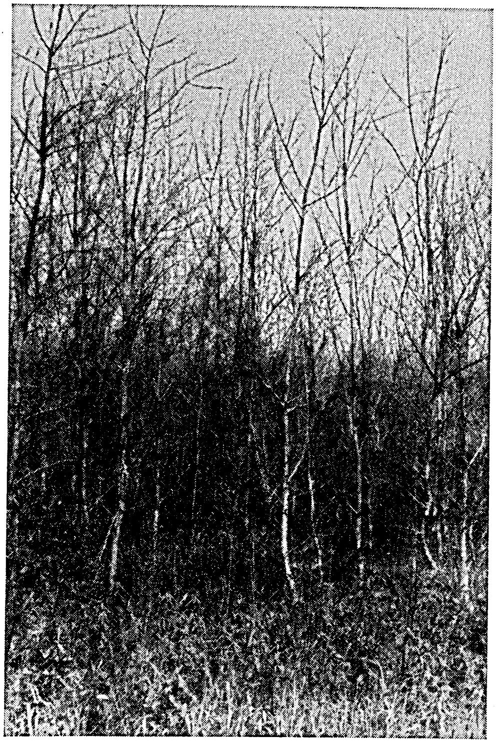

FIG. 1. COMPLETELY DEFOLIATED ASPEN, *Populus tremuloides*, NORTH OF ITASCA STATE PARK, JUNE 1937

(Dark patches are groups of caterpillars.)

been no critical studies of the progress of outbreaks and controlling factors. The purpose of this bulletin is to present observational and experimental data concerning the development of an outbreak in Minnesota and an analysis of the factors responsible for its termination. In developing the subject the following fundamental studies will be described: general life history, feeding habits and host preference, population measurement, dispersal, variations in numbers, and causes of mortality. A method of predicting the probable abundance of the caterpillars and the degree of damage also will be presented.

HISTORICAL DISCUSSION

General Historical Review

The forest tent caterpillar has been an important enemy of forest, orchard, and shade trees for many years. In fact, there are authentic records of outbreaks in the eastern United States since 1797. Baird (1) has contributed an excellent summary of reported outbreaks in all parts of the United States and Canada. In this he has shown that large populations of *M. disstria* have appeared at approximately ten-year intervals. A remarkable feature of these periodic disturbances has been their occurrence in nearly all sections of the United States and Canada at about the same time. The last general outbreak described by Baird reached its peak between 1910 and 1913. It began to subside in

1913 in the western states and a year later in the East. The following history of outbreaks of *M. disstria* since 1916 has been prepared from data in the Insect Pest Survey Bulletin, the annual reports of the Canadian Forest Insect Survey, and miscellaneous experiment station notes and reports.

The forest tent caterpillar was not generally abundant from 1914 to 1918. From 1919-1921 there were local outbreaks in British Columbia, Oregon, and Minnesota. In 1922 there were large areas of heavy defoliation in Minnesota, North Dakota, Idaho, Oregon, Maine, and Massachusetts. Except in Minnesota, North Dakota, and Oregon, the infestations reported in 1922 were again severe in 1923. In addition, the insect was found to be increasing in numbers in Connecticut, New York, New Jersey, and New Brunswick, Canada. Outbreaks continued during 1924 in many parts of Canada, particularly in Saskatchewan, western Ontario, New Brunswick, and Nova Scotia. There were local areas of complete defoliation in the Vancouver district, B. C., and also in Maine, New York, and New Jersey.

During 1925 and 1926 there were fewer reports of extensive areas defoliated, but poplars were damaged in parts of Saskatchewan, Alberta, and in the lower peninsula of Michigan. There was also some defoliation reported from North Carolina. There were only widely scattered local outbreaks in Sonoma County, California, Massachusetts, North Carolina, and Alberta and Saskatchewan, Canada reported during 1927 and 1928. Again in 1929 there were relatively few areas where heavy defoliation occurred. There were reports of moderate to heavy damage from Washington, east-central Minnesota, and British Columbia and Saskatchewan in Canada.

In 1930 the defoliated areas in Washington and Minnesota again were badly infested, and there were new localities in Utah and Virginia where there was complete defoliation. In Virginia there was complete defoliation of oak, hickory, cherry, and black gum. The caterpillars completely ignored tulip poplar and soft maple. The Washington, Minnesota, and Utah infestations reached very low levels in 1931. At the same time the worst outbreak on record occurred in Virginia. Heavy defoliation was also reported from northern Maine, Alabama, Florida, and Louisiana. The local outbreak in northern Maine continued during the summer of 1932 when it was reported as the most severe infestation ever seen in the area. Local outbreaks were also reported from Iowa in 1932, and some decrease in the population was evident in Virginia.

The year 1933 marks the beginning of another period when severe outbreaks were common in all sections of the country. During 1933 heavy defoliation was reported from Maine, Minnesota, Pennsylvania, Colorado, Utah, and New Hampshire. There were new areas infested in Virginia, but the areas previously attacked showed much lighter damage. The caterpillars were common in Louisiana, but they were much less abundant than in 1932. Canadian reports indicate that there was considerable defoliation in northern Saskatchewan in 1932 and outbreaks of great severity in New Brunswick, Ontario, and Saskatchewan during the summer of 1933. The following year the infestations reported in 1933 continued with increased acreage. There were additional reports of outbreaks in Connecticut, Mississippi, New Hampshire, British Columbia, and Wisconsin. The records for 1935 indicate further extension of the areas defoliated in 1934 with the addition of outbreaks in New York and Michigan. There was a spotty distribution of infested areas in Vermont and Louisiana and a local outbreak in Martin County, Indiana. Thousands of acres were defoliated in 1936 in many parts of the country. States reporting large areas with complete defoliation were Maine, Vermont, New Hampshire, Connecticut, Massachusetts, New York, Pennsylvania, Mississippi, Louisiana, Utah, Washington, Michigan, Minnesota, North Dakota, and Montana. There was extensive damage in Ontario and British Columbia and a moderate infestation in parts of Saskatchewan and Manitoba. The widespread outbreaks continued through 1937 with ever increasing damage. There were a few changes from the conditions existing in 1936. No complete defoliation was reported from Washington, Utah, Louisiana, Mississippi, or North Dakota. South Carolina was added to the list of states which were infested.

Beginning with 1938 a very great change in the country-wide outbreak can be seen. The caterpillar population declined sharply in all the New England states, Pennsylvania, New Jersey, Michigan, Minnesota, and South Carolina. There were still local outbreaks in Washington, North Dakota, Montana, and small areas in Pennsylvania. In 1939 the only states reporting heavy defoliation were New York, Washington, Michigan, and Oregon. There were small, local outbreaks in Montana, North Dakota, and Pennsylvania. In Canada complete defoliation was reported only from parts of northern Saskatchewan and Manitoba. At present the general outbreak which began about 1933 has subsided to a state similar to that which existed after 1926.

Outbreaks in Minnesota

Complete information on the occurrence of the forest tent caterpillar in Minnesota is not available. The general history outlined above likewise represents a fragmentary record of the insect because systematic surveys and reports have been adopted generally for only a few years. The first published report of an outbreak in Minnesota, a comment by Murtfeldt (9), tells of a heavy infestation near Lake Minnetonka which she observed during the summer of 1891. Murtfeldt also mentions newspaper accounts which indicated widespread damage in northern Minnesota. The next outbreak probably occurred about 1898. Lugger (8) states that the forest tent caterpillar was noticeably abundant and Baird (1) has recorded reports of serious infestations at about the same time in neighboring parts of Canada and Michigan. There is no complete record of the outbreak which must have appeared about 1912. Local newspapers mention caterpillars swarming over the poplars, and old settlers and Indians recall the infestation. However, there is no definite description of the caterpillars. There is some indirect evidence that there might have been a large population at this time because the pest was very abundant in Canada and in many of the eastern states. About ten years later Ruggles (13) described an outbreak in the "Park Region" of northern Minnesota. The infestation was first observed in 1921 and continued through 1923.

There was no further heavy defoliation by *M. disstria* until 1933, the beginning of the last general disturbance, except two local infestations near Park Rapids and Detroit Lakes in 1929 and 1930. These areas were small, and the outbreaks subsided rather quickly. The following description of the development of the last serious outbreak is based upon reports provided by rangers of the Federal Forest Service, the State Forest Service, County Agents, and other interested individuals. The map (Fig. 2) indicates areas where complete defoliation occurred during the development of the outbreak. Completely defoliated trees were first observed near Ely, Minnesota in 1933. There is no accurate description of the area infested at that time, but it is assumed that the outbreak was local. During 1934 the pest spread from the center near Ely, to two new areas, one west of Ely in St. Louis County and the other north of Cass Lake. The summer of 1935 showed a great extension about the areas previously infested and the appearance of completely defoliated trees in widely separated areas where there had been no damage reported before.

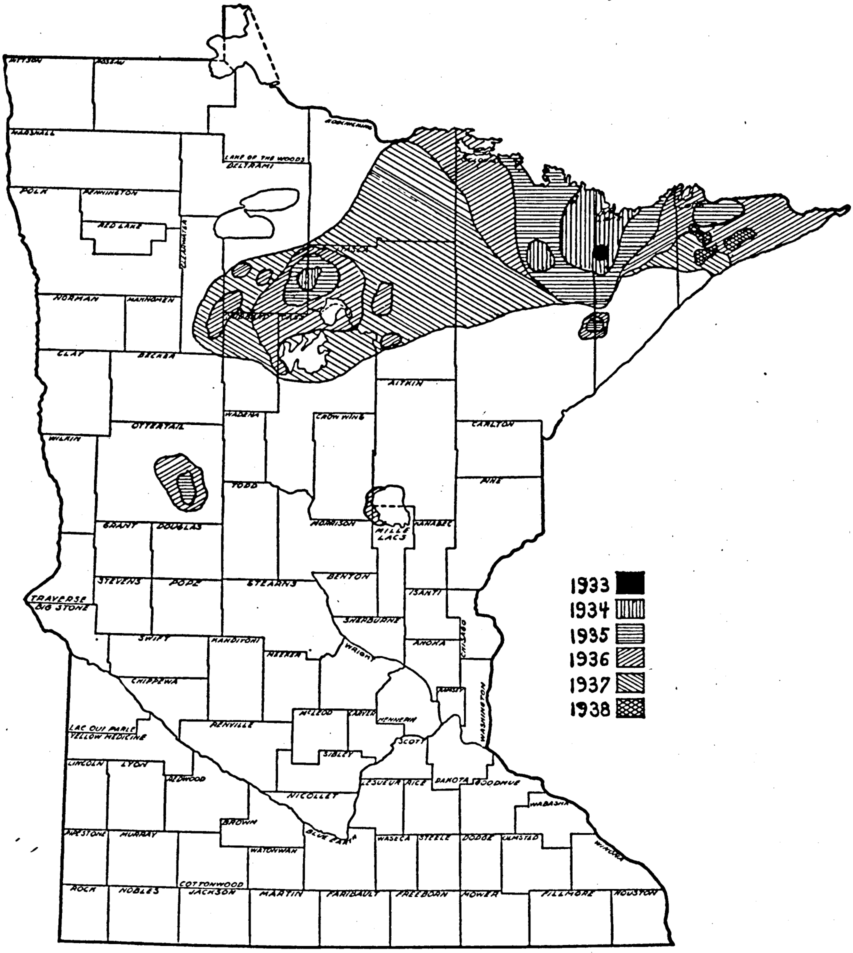

Fig. 2. Areas in Which There Was Complete Defoliation by the Forest Tent Caterpillar During the 1933-1938 Outbreak in Minnesota

During 1936 and 1937 there was a general increase in the size of the defoliated area. One local outbreak which remained isolated from the principal region was terminated in 1936. This area included stands of mixed hardwoods near Detroit Lakes and Perham. At the peak of the outbreak in 1937 there were approximately three million acres in the area where there was complete defoliation. The forecast for defoliation in 1938 indicated further spread of the infestation and continued complete defoliation in the poplar stands where the outbreak had been in progress for some time. However, there was severe damage only in three areas in Cook County in 1938 and even these populations were reduced to a very low level in 1939. The factors which were responsible for the nearly complete disappearance of the forest tent caterpillar will be discussed in a later section.

BIONOMICS

Life History in Minnesota

Young larvae first appear when poplar leaves are just beginning to unfold. The hatching date in Minnesota varies from May 5 to May 25, the time depending upon prevailing weather conditions and locality. Hatching takes place commonly during the first two weeks of May except in those areas which are influenced by Lake Superior. When first hatched, the larvae are a nearly uniform black color and bear conspicuous hairs. With each successive molt the familiar markings of the full-grown caterpillars become more evident. There is considerable variation in the time required to complete each stadium but table 1 gives a general idea of the seasonal progress of larval development.

During the first three stadia the caterpillars are constantly gregarious. The newly hatched larvae from one egg mass often cluster on one leaf or one group of small, expanding leaves. As they grow older the aggregation is distributed over more foliage because caterpillars are larger and demand more food. The data gathered at Ely and additional observations made at Itasca State Park indicate that the caterpillars begin to move about more during the fourth stadium. They feed more independently but still come together on the tree trunks when they are resting and when they are preparing to molt. Complete defoliation usually occurs first about three weeks after hatching. During the latter part of the fourth stadium the "worms" seem to come from no-

Table 1. Phenological Record of Larval Development and Adult Activity

Stages of Development	Ely, 1936	Itasca Park, 1937
Hatching	May 12	May 10
First molt	May 19	May 17-19
Second molt	May 25	May 25-27
Third molt	May 28	May 30-31
Fourth molt	June 5-8	June 7-9
Pupation	June 16-July 3	June 18-July 4
Moth flight	July 7-July 20	July 5-July 18
Eggs present	July 8	July 7

FIG. 3. LARGE AGGREGATIONS OF FIFTH INSTAR LARVAE IN TYPICAL DAYTIME RESTING POSITIONS

where and strip the trees of their leaves overnight. If the population is very large, the fifth instar larvae often crawl many yards in search of food. In this stage they cluster on tree trunks during the day (Fig. 3). Under field conditions larvae pass through five instars, but occasionally laboratory reared individuals have six instead of the usual five instars. Usually five to six weeks elapse between the hatching date and the appearance of the first cocoons.

Larvae are very restless before they start to spin cocoons. They wander about over trees and ground vegetation in what appears to be an aimless meandering. Cocoons are spun in rolled leaves of a host tree or in most any type of vegetation. Caterpillars seem to prefer to construct cocoons in folded leaves but will occasionally spin them on buildings and fences. In areas where there was complete defoliation cocoons were massed in needles of coniferous trees and in shrubs and herbaceous plants. Red maple, *Acer rubrum,* leaves were often selected because they were not fed upon by the larvae. Figure 4 shows a clump of red maple in which nearly every leaf contained from one to five cocoons.

Caterpillars require about 24 hours to construct a cocoon. When it is completed they remain inactive in the prepupal stage for about two days and as pupae for 8 to 12 days. Observations on moth emergence were made in 1936 and 1937. A total of 2,165 moths emerged in insectary cages during these studies. The cocoons in which they transformed were collected in the field a few days before the first moths appeared. In all cages the leaves were removed from around the cocoons because observations during 1935 showed that the dried leaves are unnatural and seriously interfere with successful emergence. The sex ratio of the emerging moths was 0.47 in 1936 and 0.48 in 1937. Sweeping collections made during the flight period of 1936 also showed a sex ratio of 0.48. Both males and females were represented among the first moths to emerge each year, and the average length of adult life was similar for the two sexes. The average time in days was 5.02 for males and 5.28 for females in 1936, and the corresponding time in 1937 was 5.30 and 4.91 days for males and females, respectively. The flight period lasted 9 days in 1936 and 12 days in 1937. In the field the moths were active for about two weeks. Under insectary conditions the moths mate soon after emergence. In fact, they are often seen in copulation before the wings of the females are completely dry. The females may lay their eggs within three or four hours after emergence. No extensive field observations of moth activity were made, but there was probably much more delay in mating and oviposition of unrestricted moths. Moths fly about actively in woods and are frequently attracted to lights in large numbers even when illumi-

FIG. 4. FOREST TENT CATERPILLAR COCOONS IN ROLLED LEAVES OF RED MAPLE, *Acer rubrum*

nated buildings are two or three miles from an infested area. The active flight of the moths enables expansion of infested areas to take place very rapidly. In 1937 egg masses were collected in the field daily to determine the length of the period of embryonic development. The first were discovered on July 7, and the first young caterpillars were found in eggs on July 29. Insectary studies also indicated that about three weeks are passed as developing embryos. Perfectly formed young larvae remain in the egg until the following spring. There is truly a larval diapause, although it is said commonly that winter is passed in the egg stage.

The Effect of Temperature on Larval Development

Newly hatched larvae were placed on aspen foliage in temperature cabinets in which the temperature was controlled within $\pm 0.5°$ C. Humidity in the chambers was not regulated because preliminary experiments indicated that within a range of from 30 to 70 per cent relative humidity there was little effect upon the rate of growth and feeding. Fifteen larvae were used at each of the temperatures selected for the experiment. Larger numbers were not necessary because there was very little variation in the time required for each group to complete a stadium. The results of the experiment are presented in table 2.

Above 15° C. the effects of temperature upon the duration of each stage exhibit characteristics similar to like data for other species. At 15° C. (59° F.) the larvae feed and grow slowly until they have molted for the third time. When they reach the fourth instar, they become even more sluggish and do no more feeding. Little movement and no feeding was observed at 10° C. (50° F.). The ability of the young caterpillars to feed at 15° C. is very

Table 2. The Effect of Temperature on the Rate of Growth of the Forest Tent Caterpillar

Stage of Development	Duration of stage in days at each temperature				
	30° C.	25° C.	20° C.	15° C.	10° C.
First instar	2	3	5	11	No development
Second instar	2	3	4	12	......
Third instar	2	3	9	21	......
Fourth instar	3	5	7	......*	......
Fifth instar	6	7	17	......*	......
Pupa	10	12	22	......	......
Total	25	33	63	......	......

* Lived for 30 days in fourth instar with no feeding at 15° C.

important because the average maximum temperature for May is often only a little above 60° F., and the average temperature during the feeding period of the first two instars may be between 55 and 60° F. In May, most of the defoliating is done on days when the maximum temperature exceeds 75° F.

The Quantity of Food Eaten

A study was made of feeding habits and quantity of food consumed during each larval stadium. Experiments were planned to obtain some general information about larvae and to serve as a basis for further work on population estimation and a method of predicting the amount of defoliation. Several rearing methods were tried in an effort to overcome many difficulties. Finally feeding studies were carried out in a perforated celluloid tube sealed at one end. The type of tube now used as a killing bottle is very satisfactory. The perforations were made with a hot needle and seemed to provide sufficient ventilation. The open end of the tube was plugged with a cork stopper which had a hole through it large enough for an aspen leaf petiole. After a leaf and a larva were placed in the tube, the petiole was drawn down through the hole in the stopper and the cork was forced into the tube. The other end of the cork stopper was placed in the top of a small bottle which contained water. The petiole had to protrude for at least a quarter of an inch to reach the water in the reservoir. With this type of rearing chamber there was no danger of losing the larvae, they could not stray far from the food, their excrement could be collected easily, and the food leaves remained fresh for a day or more longer than they did when entirely exposed. A cage with a forest tent caterpillar cocoon spun within it is shown in figure 5.

The quantity of food consumed per day was measured by tracing the outline of a leaf before the caterpillars fed and again

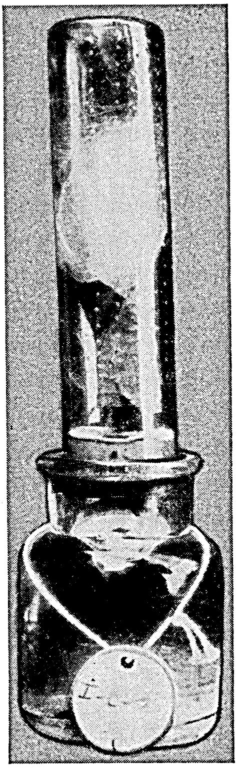

FIG. 5. REARING CAGE USED IN FEEDING STUDIES. COCOON AND PORTION OF OLD LEAF ARE ENCLOSED

after the leaf was removed. The area destroyed was measured in square inches with a planimeter. Excrement was collected each time the food was changed. During the first three instars food was changed only when new leaves were needed and when caterpillars molted. Five caterpillars were used in each rearing cage during the first three stadia, and single caterpillars were used during the last two feeding periods. Some of the feeding experiments were carried on with young larvae hatched from eggs which had been kept in cold storage. These larvae were beginning to feed from one to two months later than larvae which had started in the field. There was some difficulty in rearing them until it was noticed that they could not feed easily on mature poplar leaves. When they were offered new leaves from the terminal growth of young trees they had no trouble. The area of poplar leaves eaten during each instar and the total area consumed per caterpillar is given in table 3.

The data presented indicate clearly the reason for the sudden increase in the rate of defoliation upon the appearance of the fourth and fifth instar larvae. The very unequal distribution of the instar feeding rates can also be described in terms of the number of average sized leaves eaten. During the first three stadia a caterpillar consumes about the equivalent of one half leaf. The fourth instar caterpillars eat a little over one entire leaf, and during the last stadium about seven leaves are destroyed. Complete defoliation may occur on trees in which there were no eggs or small larvae because considerable migration commonly takes place during the period of heaviest feeding.

Under laboratory conditions six instars were observed when feeding studies were made in 1938. However, there was no evidence of more than five instars for either sex in the caterpillars collected in the field during the same season. Some data were collected on the feeding habits of these irregular caterpillars. The average number of square inches of leaves eaten by the caterpillars were as follows: First instar, 0.048; second instar,

Table 3. Area of Poplar Leaves Consumed During the Period of Larval Development

Instar	No. larvae	Average leaf area in square inches	Percentage of total food consumed
I	13	0.05 ± .006 S.E.	0.23
II	11	0.17 ± .026	0.78
III	10	0.75 ± .034	3.42
IV	10	2.92 ± .400	13.34
V	10	18.00 ± 2.89	82.23
Total	......	21.89	100.00

0.19; third instar, 0.76; fourth instar, 1.91; fifth instar, 3.69; and the sixth instar, 16.4. The average total area consumed was 22.99 square inches as compared with 21.89 square inches for the larvae with only five stadia. Measurements show that there was practically no difference in rate of feeding of the two groups during the first three stadia. Both males and females were produced by larvae which had only five instars, but only females emerged from those which had six.

Measurements of Frass Production

Quantitative collections of caterpillar frass have been used to estimate forest insect numbers when other methods are impracticable. Nolte (10) and others have found it possible to determine the species, the stage of development, and the relative density of the larval population from an examination of frass collections. Frass samples have been taken by placing funnels, cloth traps, or sticky paper beneath the crown of infested trees. These methods have all been satisfactory and have been recommended by various investigators.

With regard to procedure subsequent to collection of pellets there has been some difference of opinion. Schwerdtfeger (16) in calculating the abundance of *Dendrolimus pini* L. used weight of frass accumulated in a unit of time. This method is not accepted by Gösswald (4), who counts the number of frass pellets rather than determining the weight. He used pellet counts because the number of frass pellets produced vary less than their weight and because weighing technique requires much more labor. All extraneous matter such as dead caterpillars, leaves, and other debris must be removed before weighing. In addition, collections have to be transported to the laboratory where they may be dried. All three of these investigators have emphasized the important effects of food and weather conditions on the size and number of frass pellets. Gösswald (4) made a detailed study of the number of pellets produced when caterpillars were exposed to various combinations of temperature and moisture. He found that temperature has a much greater effect than the relative humidity.

In this study frass examination included only counts of the number of pellets and a determination of the average weight and linear dimensions of the pellets from larvae in each instar. Frass was collected from caterpillars reared in an insectary, as described in the discussion of feeding, and oven-dried at 100° C.

Table 4. Average Frass Pellet Counts and Measurements for Each Larval Instar of *M. disstria*

Instar	Number per Individual	Weight in mg.	Length in mm.	Width in mm.
I	197.1	.008	.21	.13
II	140.0	.016	.42	.22
III	124.2	.076	.56	.29
IV	183.8	.271	.89	.52
V	295.1	1.643	1.69	1.23

Length and diameter measurements were made with a micrometer eyepiece on samples of 100 pellets. The results of the study are summarized in table 4. Samples of frass produced during each instar are illustrated in figure 6.

Data concerning the number of pellets and their total weight during each stadium are presented only to indicate the relative amounts produced. Further information on the daily production as affected by weather conditions is necessary before the weight and number can be used for an accurate measure of population. The measurements of the average length and width of

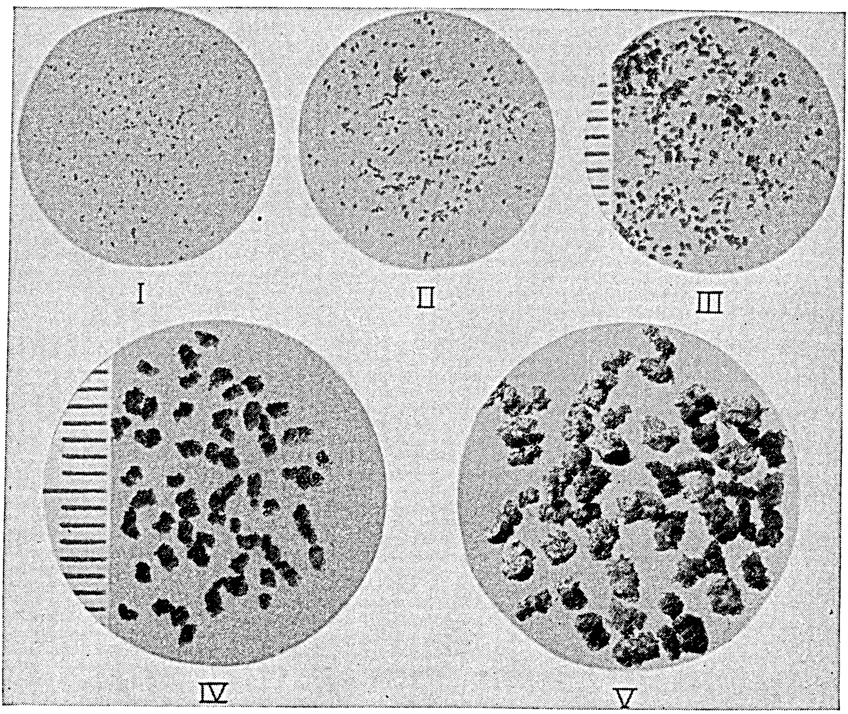

FIG. 6. SAMPLES OF FRASS PELLETS FROM EACH LARVAL INSTAR OF *Malacosoma disstria*

the pellets indicate clearly that the stage of development can be determined easily from frass collections. Small caterpillars are not easily seen in large trees, but their presence and relative abundance can be determined when sampling trays are placed beneath the trees. Although there was no intensive field study made of frass sampling in this investigation, some trays were set out to determine the practicability of the method. Some of these trays were used in connection with spraying experiments and the number of pellets which fell on them showed the reduction in feeding on the sprayed trees remarkably well. Other cloth trays were placed under trees which were known to have different numbers of egg bands in them. The number of pellets collected indicated the differences between trees with large and very small numbers of eggs, but there was considerable variation in the intermediate groups.

Nolte (10) has pointed out that sometimes the frass sampling method cannot be used successfully unless only one species of insect predominates in the tree population. There is always the danger of confusing the frass pellets produced by one species with those from another. Nolte has demonstrated also that it is particularly difficult to distinguish pellets of various species during the early stadia. The importance of these observations was realized early in the progress of this study, and frass produced by other species of defoliators has been collected for further study.

Host Tree Preference and Food Favorable for Young Larvae

The aspen, *Populus tremuloides,* was the principal forest tree attacked in northern Minnesota. This species is distributed generally throughout the area and is often found in nearly pure stands. Other species of trees were also attacked readily, and the order of preference was usually as follows: hard maple, *Acer saccharum;* basswood, *Tilia americana;* red oak, *Quercus borealis;* bur oak, *Quercus macrocarpa;* paper birch, *Betula papyrifera;* and American elm, *Ulmus americana.* In some areas the caterpillars were so numerous that they fed upon nearly all green foliage including garden crops and even larch, *Larix laricina.* In locations near Lake Superior in 1936 the caterpillars stripped the foliage from strawberries, cabbage, peas, beets, and potatoes. The only tree which was consistently avoided was the red maple, *Acer rubrum.* This species became very conspicuous at times because it often bore leaves when all the aspen and birch in the stands were completely defoliated. Although it was always free from attack by feeding caterpillars, the red maple did not escape entirely. As illustrated in figure 4 the leaves were used by the larvae when they constructed their cocoons.

When poplar, birch, and bur oak trees were present in the same stand, the caterpillar fed first in the poplars, then in the oaks, and later in the birch. Both laboratory and field studies were made to determine the reasons for this. Two conditions must be satisfied before there can be feeding damage during the first two or three instars or before the caterpillars move from one tree to another. Egg masses must be present on the tree, and the caterpillars must find suitable foliage soon after they hatch. The common aspen is very favorable in both respects because the eggs are deposited readily on the small twigs of this tree, and the caterpillars can feed upon the leaves as soon as the buds break. In most seasons the eggs hatch and aspen leaves appear during the same week. The oak is unfavorable early in the feeding period for two reasons. Few eggs are deposited on the twigs of bur oak because of their large diameter. An average of over 500 aspen twigs upon which egg bands were found measured 0.118 inches in diameter. They ranged from 0.064 inches up to 0.168 inches. The twigs of slow-growing bur oak are usually greater than 0.175 inches in diameter. The moths may shun these trees for other reasons, but the twig diameters offer a possible difficulty. A second unfavorable condition found in bur oak is the delayed opening of the buds. The first leaves often appear a week or more after the caterpillars have hatched. However, feeding tests made in the insectary indicate that the young leaves are favorable food.

Two factors seem to be responsible for the absence of young larvae in birch. First, very few eggs are deposited on birch twigs. The birch twig diameters present no obstacle so apparently the moths are not attracted by these trees. Second, the first and second instar larvae cannot survive on the young foliage of birch. The small caterpillars are unable to feed and move about on the sticky surface of the small leaves.

In spite of the small amount of damage observed in both oak and birch early in the season, they may be completely defoliated by the older caterpillars toward the end of the feeding period. Birch is attacked by caterpillars after they move from stripped poplars. The defoliation of birch often proceeds from the lower part of the crown upward. The top of aspen crowns are nearly always defoliated first.

The Effects of Starvation During the Last Instar

During the summer of 1936 there were localities along the north shore of Lake Superior where the caterpillars completely exhausted their food supply. The food shortage became acute before the caterpillars were half through the fifth instar. As a result hundreds of thousands died from starvation. They often piled up several inches deep in the road ditches. The population decrease caused by starvation was an obvious effect, but it was believed also that some of the adults developing from larvae which had been partially starved might have been influenced. For this reason insectary experiments were set up to determine larval resistance to starvation and the effects of partial larval starvation on the adults. Four lots of 50 larvae were selected just after their fourth molt. One lot was placed on aspen foliage as a control, two lots were placed in cages without food, and the third lot was allowed to feed for three days before they were deprived of food. One group of caterpillars was never given food, and the other group which did not feed at the start was treated in two ways. Twenty-five larvae were starved for two days and then placed on aspen leaves, the remaining 25 were starved for five days before being fed.

All of the control caterpillars and those which were starved for only two days produced moths. None of the larvae which were not allowed to feed survived long enough to pupate. However, all but ten of those which fasted five days reached maturity. In the fourth group, the caterpillars which fed for three days, the following records were obtained: 16 died before spinning a cocoon, 6 formed cocoons but did not pupate, 4 died in the pupal stage, and 24 emerged as moths. The control caterpillars fed for seven days during the fifth stadium, and so the fourth experimental group fed for less than half the usual time. The partially starved larvae started to spin their cocoons on the same day as the normal caterpillars. In this case pupation certainly was unrelated to the nutritional state. The starved larvae were much smaller than the well-fed controls, and the adults which they produced were also much smaller than the normal moths. Upon dissecting the two groups of moths it was discovered that the normal females contained an average of 174 eggs as compared with 97 for the partially starved group. A sample of moths which were collected in the field at the same time contained an average of 152 eggs. From these few experiments it can be seen that complete inanition during the fifth stadium results in death, but partial starvation, which occurs whenever caterpillars are forced to wander in search of food, may produce all degrees of injury.

It was mentioned that starvation occurred in the field populations observed near Lake Superior. Egg masses were collected in this area when the fall egg survey was made. A sample taken between Grand Marais and Hovland provides field evidence of the effects of starvation on egg production. The sample showed an average of 99.6 eggs per mass while the average for the entire infested area was 143.9 eggs. The following year there was a marked reduction in the amount of defoliation in this area. The population decrease was due largely to the high caterpillar mortality and to some extent to the lower egg production, but there was another factor present related to the former. The parasite population was already increasing, and the reduction in caterpillar numbers by starvation raised the percentage of parasitism over 15 per cent above that in other nearby areas where there was little evidence of starvation.

POPULATION MEASUREMENTS

One of the chief aims of this investigation was the evaluation of various environmental factors which might have some influence on the size of populations of *Malacosoma disstria.* To do this it was necessary to decide upon methods of comparing populations, and several possibilities seemed worth investigating. The results of the study will be presented in the following descriptions of various procedures.

Cocoon Sampling

The cocoons of the forest tent caterpillar usually are constructed in folded leaves of the trees in which they have been feeding or in leaves of ground herbs and shrubs. When the trees have been defoliated completely, the cocoons are present in all types of ground vegetation, including ferns and grasses. The cocoons are very easy to see and collect, but it is not always possible to make a population estimate on the basis of one simple procedure. There are a number of conditions which determine the most satisfactory method. Among these are degree of defoliation, uniformity of the ground cover, size of the host trees, and particular reason for sampling the population. The cocoon sampling methods used were the following: time collections, temporary sample quadrats, permanent sample quadrats, general collecting, and tree collections. The first four methods can be used when all the cocoons are found in the herbs and shrubs. However, they give a very incomplete picture when there is any foliage left on the trees because under this condition at least part of the cocoons will be found in the trees. In two plots where the cocoons in single trees were counted and compared with the number in ground quadrats the counts showed 27 and 676 cocoons in the trees in contrast to 4.3 and 54.0 in the quadrats.

Time-collections were taken by hand-picking the cocoons for a definite length of time, usually three minutes. The collector walked through the infested stand at a rate as constant as the vegetation and topography would allow. The principal chances for error occurred when the population was very large or extremely small and when the undergrowth was irregular. When there were 70 or more cocoons per square meter, the collector could not pick fast enough to indicate the difference between this density and a density of 50 or 80 cocoons per square meter. A similar difficulty appears in nearly all attempts to make time-collections. At very low population densities the cocoons are often difficult to find and the collector invariably "takes time" to search for them instead of picking only those encountered by chance. Irregular vegetation also affects the counts by introducing some manual difficulties in collecting the sample. In spite of the limitations indicated the results of time-collections compare quite favorably with samples taken by another method. Such a comparison is made in table 5.

Temporary sample quadrats were used when greater accuracy was desired. These were laid out at random or at intervals of ten paces along a line. In either case the northwest corner of the quadrat was established at the point where the collector's foot rested on the last pace. A hinged meter stick was used to mark

Table 5. A Comparison of Time-collections of Cocoons and the Average Number in Three Permanent Square Meter Quadrats

Plot No.	Time-Collection Counts	Square Meter Quadrat Counts	Plot No.	Time-Collection Counts	Square Meter Quadrat Counts
1	0	0	6	62	31.2
2	2	0	7	84	54.6
3	8	0.3	8	87	60.0
4	22	9.2	9	95	61.9
5	35	13.8	10	98	55.5

the boundaries of the quadrat. Because the caterpillars showed some selection in seeking a place to form their cocoons at least ten samples had to be taken to give a reasonably accurate count. Hazel brush and small red maple trees were selected more often than low ground herbs. Permanent quadrats were laid out in each tenth-acre plot used in this investigation. Three quadrats were placed in line diagonally across the plot and equidistant from each other. These quadrats were established to provide a place for reference over a period of years. They were marked in 1937, and since that time there have been no cocoons found in the plots.

General collections were made in the tenth-acre plots and in numerous other areas to obtain material for studies of parasite abundance, moth emergence, etc. These collections were necessary to insure large enough samples, particularly in stands where the population density was low. Tree sampling for cocoons was done in three ways. The cocoons were collected or merely counted by bending down small trees. Somewhat larger trees which could not be bent were examined from the ground and the cocoons counted with the naked eye or with the help of binoculars. Large poplars, 30 feet high or taller, were cut down and the cocoons removed. Frequently the caterpillars will form clusters of cocoons which make it necessary to collect the folded leaves and open them before an accurate count can be made. Since it is usually necessary to cut all trees which cannot be bent to examine them for egg bands, cocoon counts can be taken at the same time without cutting additional trees.

Egg Sampling

An estimation of the number of egg bands per tree seemed to be a very important measurement for purposes of prognostication. The eggs deposited in July represented not only the reproductive effort of the currently emerging moths but also could be used as indicators of the probable caterpillar population for the following year. Egg mass collections were also necessary to complete studies concerning the importance of winter mortality in the subsidence of the outbreak. For these and other similar reasons it was desirable to have a means of sampling the egg population. In nearly all of the egg surveys a sample of ten trees of approximately average D. B. H. (diameter breast high) for the stand were cut and the twigs examined for egg bands. In some cases a larger number of trees would have been better,

Table 6. Egg Counts Made by Means of Binocular Field Glasses Compared with Actual Numbers

Number of Egg Bands				
Observers		Actual Count on Felled Tree	Differences	
No. 1	No. 2		No. 1	No. 2
6	7	16	−10	− 9
5	9	4	+ 1	+ 5
3	4	14	−11	−10
3	6	33	−30	−27
14	12	61	−47	−49
13	17	24	−11	− 7
10	6	13	− 3	− 7
5	8	10	− 5	− 2
8	12	37	−29	−25

but some limitation had to be placed on tree felling. When young trees (under 2 inches D. B. H.) were studied, they could be bent down and many more sampled. The tree-cutting method seemed quite wasteful and sometimes very undesirable. Other methods were tried, including counts made from the ground with binocular field glasses. When this method was attempted in the field, it was found to be inaccurate. The tests were made after the leaves had fallen when two observers surveyed each tree and recorded the number of new egg bands. Afterward the trees were cut and the actual number of eggs determined. Table 6 shows the results of field tests of the binocular method.

The tabulated data indicate clearly that the ocular estimate of egg masses is unreliable. In general, the observer tends to underestimate the number of egg bands. They are often nearly the color of the twigs, and they can be confused easily with bud scars. In spite of the discouraging results of the test of the method it still has some merit. Trees in parks, around homes, and near resorts can be surveyed from the ground when cutting would be prohibitive. The counts, although not accurate, always showed the presence of egg bands and usually gave a relative value which could be used as a means of indicating whether or not spraying would be necessary.

Sampling of Larvae and Adults

During this investigation little attempt was made to conduct extensive surveys of the caterpillar population. However, some techniques were studied to explore their possibilities. The use of collections of frass pellets has already been mentioned as a method for determining the age and relative abundance of the caterpillars. When small trees are being studied, the caterpillars can be shaken down on a ground cloth. The tree-shaking procedure is very satisfactory for late third instar larvae and older caterpillars, but the younger larvae fall on a silk thread and fewer of them reach the cloth.

A third method was used for late fourth and fifth instar caterpillars. The older larvae congregate on the trunk and larger branches during the day. There they can be counted and the results expressed in numbers per tree or numbers per acre. This method can be used on trees of nearly all sizes, and it is particularly useful when the population is low.

Although no quantitative collections of adults were made during this investigation, they would be important. Light traps do attract large numbers of moths, but there is no information published concerning the reliability of the method. Such traps may prove to be useful in demonstrating the presence of the pests when the population is so low that immature stages are easily overlooked. The method also should be of some value in the study of moth flight.

POPULATION SURVEYS

Field collections of eggs and cocoons were made from 1936 through 1938. Many of the samples were taken by the author and field assistants but invaluable help was afforded by other groups. Rangers employed by both the State and Federal Forest Services made systematic collections which were forwarded to the University of Minnesota. Surveys were made to provide very necessary information concerning the progress of the outbreak. They were also the basis for much of the material which will be presented on natural control.

Egg Survey Records

Thousands of egg bands were collected in many of the areas under observation. These large numbers were very desirable because they provided abundant study material, but the time required to count the number of eggs in each band made small samples necessary. The number of eggs in each band was approximated by counting the number of eggs around the circumference and multiplying by the number of rows of eggs in the mass. The figures in table 7 indicate the reliability of the method.

Table 7. A Comparison of the Estimated Number of Eggs in Bands and Total Counts

Number of Bands	Average Total Count	Average Estimated Number	Number of Bands	Average Total Count	Average Estimated Number
10	126.5	124.8	10	145.8	152.9
10	153.9	159.0	10	135.5	144.9
10	140.7	138.6	10	172.3	170.6
10	208.2	200.0			
			Average 10	154.7	155.8

There was such a small difference in the numbers obtained by the two methods that total counts were used only when the samples were very small or when the egg masses were formed irregularly. In addition to the total number of eggs in each band it was desirable to have information concerning egg mortality. Inspection of large numbers of samples was facilitated by cutting the tops from three rows of eggs on opposite sides of each mass. After a number of experimental counts it was found that 60 masses, those selected at random from large samples, gave reliable data. The remarkable agreement between the strip counts and the total counts of eggs is shown in the following statistics taken from an examination of 60 egg masses. Two strips showed average percentages of 17.5 ± 6.5 dead eggs, 77.08 ± 8.4 larvae, and 5.2 ± 4.1 parasites. Total counts made on the same bands showed average percentages of 17.61 ± 8.2, 78.61 ± 8.6, and 3.58 ± 2.5. The number of eggs in the strips averaged 40.1 per cent of the total number of eggs. The most consistent thing about the parasites was their variability. This is shown by the large standard error which was found by both methods.

The embryonic development of *Malacosoma disstria* is completed about August 1. Likewise, the parasites are well-developed larvae by early fall. Since all the egg mass collections were made during the winter and spring one could determine easily the number of dead eggs and larvae, the number of parasites, and the number of normal larvae.

Eggs were sampled in several localities representing areas in which a variety of conditions could be found. The conditions varied with respect to tree size, stand density, number of years of heavy defoliation, and seasonal weather. The areas included in the survey are numbered and listed in table 8. In the following discussion the specific localities will be referred to by number only. In most cases the recorded number of years of heavy or complete defoliation is probably accurate. However, areas near the sampled plots may have had a somewhat different history

Table 8. Descriptions of Areas Used in the Forest Tent Caterpillar Egg Mass Survey with Some Stand Characteristics

Locality Number	Locality Description	Average D.B.H. of Sampled Trees			Number of Years of Heavy Defoliation Through 1938
		1936	1937	1938	
1	5- 62- 1	......	......	4.0	2
2	25- 62- 2	7.3	6.2	7.0	3
3	29- 65- 2	4.4	5.1	5.4	2
4	32- 59- 4	5.6	5.2	......	2
5	30- 57-11	7.7	8.2	6.5	4
6	31- 62-11	4.8	7.4	6.1	5
7	19- 65-13	4.5	5.2	5.5	3
8	5- 61-15	4.0	4.2	......	3
9	18- 63-16	4.4	4.2	......	2
10	24- 59-17	5.0	4.6	5.2	4
11	34- 69-21	3.5	3.6	......	3
12	23- 59-26	4.9	5.8	......	4
13	5-150-28	2.2	3.6	......	2
14	19-146-29	8.9	2.6	......	3
15	20-148-30	4.4	4.5	......	3
16	34-148-30	5.9	6.1	......	2
17	9-147-35	5.2	5.4	......	3
18	24-144-36	5.0	4.7	......	2

because in the years of initial complete defoliation there was a spotty distribution of very dense populations. The record of egg mass numbers, size, and condition is shown in table 9. The size of the trees must be kept in mind to evaluate the relative numbers of egg bands per tree. The size of the trees, the amount of foliage, and the number of stems per acre all influence the interpretation of the egg mass counts.

The number of egg bands varies greatly from one area to another. The greatest number found in any one tree was 429. The variation from one tree to another in the same stand is often large, but the changes in population density as indicated by the abundance of egg bands show a quite consistent trend. In the 14 areas sampled in 1936 and 1937 ten showed a decrease in the number of masses in 1937. All three plots sampled in 1937 and 1938 showed a tremendous decrease in 1938. Of the four areas in which there was some increase there had been three years of heavy defoliation in two of them and only two years of heavy defoliation in the others. In one of the former, locality No. 2, there was a very small increase which is not statistically significant.

The changes in egg numbers for more than three years are shown in records obtained in area No. 6. From 1934 through 1938 the counts were as follows: 25, 33, 52, 7, and 0. The evidence presented indicates that population seldom increases much for

Table 9. Records of the Condition and Abundance of Egg Bands as Determined from Samples Collected, 1936-1938

Locality Number	Number Examined			Dead Eggs			Dead Larvae			Parasites			Living Larvae			Egg Masses Per Tree			Eggs per Egg Mass		
	'36	'37	'38	'36	'37	'38	'36	'37	'38	'36	'37	'38	'36	'37	'38	'36	'37	'38	'36	'37	'38
1	......	......	7	......	......	14.9	......	......	0.2	......	......	13.8	......	......	71.1	......	......	.7	......	......	127.9
2	60	50	6	22.3	8.6	12.1	4.3	0.1	0	4.7	5.7	3.9	65.6	85.6	84.0	88.2	89.7	.6	99.6	120.9	141.6
3	60	50	......	39.8	7.5	......	3.8	0	......	4.2	15.5	......	52.2	77.0	......	18.2	12.2	0	134.5	155.3	......
4	42	9	......	24.1	11.0	......	1.4	0.9	......	2.0	11.2	......	72.5	76.9	......	9.4	0.9	0	143.5	151.2	......
5	30	50	4	33.0	9.8	19.4	2.1	0.1	0	4.1	8.4	9.3	60.8	81.7	71.3	26.3	16.8	0.4	138.1	169.6	187.0
6	60	37	......	32.8	5.7	......	4.0	0	......	0.9	12.7	......	62.3	81.6	......	52.1	7.4	0	150.2	170.9	0
7	60	25	3	37.5	16.8	31.2	12.4	0	0	2.4	10.0	7.5	47.7	73.2	61.3	22.0	2.7	0.3	131.0	166.1	200.3
8	60	50	......	53.9	12.2	......	3.8	0	......	1.1	2.4	......	41.6	85.4	......	37.8	13.5	0	171.7	154.0	......
9	60	50	......	50.0	14.1	......	6.7	0.2	......	1.3	9.5	......	42.0	76.2	......	......	11.8	0	140.0	168.8	......
10	......	......	2	......	......	22.3	......	......	0	......	......	4.7	61.9	......	73.0	9.7	......	0.2	163.5	......	170.5
11	60	50	......	41.2	2.7	......	4.2	0	......	3.2	7.0	......	51.4	90.3	......	16.7	32.2	0	151.2	119.1	......
12	60	50	......	24.6	2.7	......	7.2	0	......	2.3	6.9	......	65.9	90.4	......	39.7	24.8	0	143.0	133.2	......
13	30	28	......	25.9	5.0	......	5.0	0	......	0.3	3.4	......	68.8	91.6	......	4.2	13.8	0	172.8	169.6	......
14	......	......	......	......	......	......	......	......	......	......	......	......	75.1	......	......	83.5	11.5	......	......	......	......
15	60	50	......	22.1	6.5	......	3.6	0	......	2.3	2.5	......	72.0	91.0	......	78.9	83.3	0	124.6	130.1	......
16	60	50	......	24.7	4.6	......	6.3	0	......	1.7	2.6	......	67.3	92.8	......	146.3	76.7	0	141.2	153.3	......
17	90	50	......	29.4	12.6	......	6.2	0	......	0.9	3.1	......	63.5	84.3	......	36.5	4.7	0	174.1	97.4	......
18	......	......	......	......	......	......	......	......	......	......	......	......	73.6	......	......	63.6	......	......	170.9	......	......
Average				32.9	8.6	19.9	5.1	.09	.01	2.2	7.2	7.8	57.8	84.1	72.1	45.8	26.1	0.4	146.5	147.1	165.4

more than three years after the first noticeable defoliation, although complete defoliation may occur for four or five years. The numbers of old egg bands which are often present give no accurate measure of the numbers deposited the previous year or years. Egg masses deposited near Itasca State Park were marked in 1936 and their condition observed during the following two years. There was so much variation that no consistent trend could be found. However, some generalizations can be made. Nearly all egg bands placed on dead twigs remained for three years. Those deposited on succulent, growing terminals were nearly all gone by the end of the following summer, and those on smaller twigs persisted from one to three years.

There was also considerable change in the size of the egg bands during the three-year period. In nine of the fourteen areas the masses were larger in 1937 than in 1936, and in all of the plots in which eggs were present for three years those collected in 1938 were still larger. The samples taken in 1938 were very small, but all of the bands were above the average size for the two previous years. The number of eggs in different egg bands varies greatly as the average figures in table 9 suggest. The extremes found in the study of over 10,000 bands were 15 and 327. In Minnesota the average number of eggs is approximately 150, but records from eastern states indicate that the average may be nearer 200 in other regions of the country. In localities Nos. 2 and 17 starvation very likely caused the low rate of fecundity in 1936 for the former and in 1937 for the latter. In the other localities no field observations are available which might explain the increase or decrease in the number of eggs. Because of the great variation in the egg mass size some differences are due undoubtedly to errors of estimate.

Table 9 also shows that the samples of egg bands varied in certain other respects. The most striking differences which appeared among the 18 localities are found in records of egg mortality, although the less significant numbers of dead larvae and parasites also vary. The percentage of living larvae per egg mass gives a summary expression of the total mortality at the time when the collections were made. In nearly all localities there was the greatest survival in 1937. The causes of death and their importance during this outbreak will be analyzed later. However, the subject of mortality during the larval diapause is very pertinent because the number of larvae hatching in the spring is usually the same as the number of living larvae in the fall.

Predicting the Probable Degree of Defoliation

The data presented above represent an important portion of the general picture, and they have other values as well. They can be used in predicting the probable caterpillar population and the amount of defoliation which may be expected. Other information, of course, is necessary, some of which has been presented. The necessary facts are the following: the number of living larvae per tree, the amount of foliage eaten by each caterpillar, and the number of leaves present on the tree in question. The number of larvae per tree can be calculated from the data in table 9; namely, the number of eggs per egg band, the percentage survival, and the number of bands per tree. The feeding capacity of the caterpillars is found in another section and amounts to about eight and one-half leaves per individual, this number having been calculated from the average leaf area of 21.89 square inches consumed by each caterpillar and an average mature leaf area of 2.5 square inches. The young larvae do feed on young leaves, but most of the leaves have attained full size by the time the caterpillars reach the fourth instar.

An estimate of the number of leaves per aspen tree was based upon two measurements, the first of which involved the selection and cutting of trees in a variety of diameter classes. The number of clusters of leaves on the entire trees was counted and the average number of leaves per cluster estimated from a random sample of 100 clusters. The D. B. H. of each tree was measured along with a measure of the crown height. In the second method the number of leaf buds was counted during the winter instead of the number of leaf clusters. This data was obtained through the courtesy of Mr. Le Barron of the Lake States Forest Experiment Station. The two methods gave about the same results with perhaps a slightly greater number for the bud counts. An estimate of the crown volume or total area might have increased the accuracy of the estimate, but the need for a practical field method made such a procedure undesirable. Within any one diameter class the number of leaves varies with the crown height but in such a way that use of the measure does not add much of value. In most of the plots codominant trees were used for egg sampling and such trees show the greatest uniformity in crown dimensions. Several hundred clusters of leaves from trees in various diameter classes gave an average of about six leaves per cluster in undefoliated trees. This average number was used in calculating the number of leaves per tree shown in table 10.

Table 10. The Estimated Number of Leaves Per Tree in Several Diameter Classes of *Populus tremuloides*

D. B. H.	Number Leaves	D. B. H.	Number Leaves
1.0	2,000	3.5	10,000
2.0	5,000	4.0	12,000
2.5	7,000	5.0	15,000
3.0	9,000	6.0	20,000

Recently Potts (12) has described a method of determining the quantity of foliage per acre of woodland; however, the method could not always be used because computations are based upon applications of lead arsenate spray.

The estimated amount of foliage is expressed in round numbers because there is a variation of about 15 per cent in the counts of leaves of trees with a D. B. H. of over 3.5 inches. Only a few trees with a D. B. H. of more than 6.0 inches were examined. These were all codominant trees in even-age stands. One with a D. B. H. of 7.2 inches had about 18,000 leaves, one 8.5 inches D. B. H. had 22,000 leaves, and one 9.7 inches D. B. H. had about 30,000 leaves. The latter was the greatest number found on any tree.

In the following records, table 11, the data necessary for the prediction of defoliation are listed for localities for which field reports of damage are available. The amount of defoliation expected is represented by the ratio of the number of leaves present to the number which probably would be eaten. The degree of damage is described in these three categories: light, evident feeding damage but no complete defoliation of any part of trees; medium, conspicuous defoliation but only top completely stripped; and heavy, complete defoliation. The test of the prediction method presented in table 9 is based upon egg surveys in the fall of 1936 and reported damage in the summer of 1937. The results for 1937 and 1938 were so much influenced by mortality factors in the spring that the predictions were mostly too high.

Complete defoliation was reported in all areas where the ratio of leaves present to leaves predicted to be destroyed was greater than 1:1. There was not as much difference between the light and medium ratios although, in general, the trend was about as one might expect if the method were to be at all reliable. In locality No. 12 the defoliation ratio indicated complete defoliation, and yet the damage was reported as medium. There is no explanation for this. The defoliation reported in 1938 for those areas in which eggs were collected in the fall of 1937 further confirms the general value of the predictions. In areas 2, 5, and

Table 11. The Data Used for the Prediction of Caterpillar Numbers and Degree of Defoliation and the Results Compared with Subsequent Field Operations

Area Number	Tree Size in D.B.H.	Number Egg Bands per Tree	Number Living Larvae	Estimated Number of Leaves	Number of Leaves to be Eaten	Defoliation Ratio	Degree of Damage
2	7.3	88.2	5763	25,000	49,000	1:1.9	H
3	4.4	18.2	1330	13,000	11,000	1:0.84	L
4	5.6	9.4	977	18,000	8,000	1:0.44	L
5	7.7	26.3	2208	25,000	19,000	1:0.76	M
7	4.5	22.0	1383	13,000	12,000	1:0.92	L
8	4.0	37.8	2745	12,000	23,000	1:1.91	H
11	3.5	16.7	1309	10,000	11,000	1:1.10	H
12	4.9	39.7	3775	15,000	30,000	1:2.0	M
13	2.2	4.2	477	5,000	4,000	1:0.80	M
17	5.2	36.5	4120	15,000	35,000	1:2.3	H
18	5.0	63.6	7999	15,000	68,000	1:4.5	Y

7 the ratios were 1:3.9, 1:0.66, and 1:0.20, respectively, while the defoliation reported was heavy, medium, and very light. In these areas large numbers of young larvae were not killed in the spring as they were farther west. This indicates that there are some extrinsic factors which may influence the success of a prediction as well as the inherent chances for error in the calculations. One such factor may occur often. For instance, a sample might be taken in a stand with few eggs present but adjoining a heavily populated area. During the ensuing year the trees in the stand might be completely defoliated by caterpillars which move in after they have exhausted their food supply elsewhere.

In practice one would think of predicting defoliation simply on the basis of the number of egg bands per tree and the average size of the trees. The figures in table 12 represent the number of egg masses necessary to cause complete defoliation under average conditions in Minnesota.

If the values presented in table 12 had been used in predicting the defoliation in 1937, there would be some difference from the predictions given. The difference would be due to the fact that there was a very high egg mortality during the summer of 1936 which reduced the number of living larvae per egg mass to below the average of 125 used in preparing table 12. This method of predicting probable caterpillar abundance can be used to designate

Table 12. The Number of Egg Bands Necessary to Bring About Complete Defoliation in Trees in Various Diameter Classes

D.B.H.	Number of Egg Bands	D.B.H.	Number of Egg Bands
1	2	4	11
2	5	5	14
3	9	6	19

localities where control may be desirable only when no natural calamities interfere with the population survival. That catastrophes are likely to occur is well illustrated in Minnesota where heavy defoliation was predicted for 1938 and yet there was very little damage in all but a small part of the infested area.

Cocoon Survey Results

Quantitative samples of cocoons were not taken throughout the entire infested area. Instead, general collections were made in most localities to obtain mortality data, and the quantitative counts were made in only one intensive study area, Itasca State Park. Counts were made in seven tenth-acre plots during the summer of 1937. These plots differed from one another particularly with respect to the amount of defoliation and the number of years in which there had been complete defoliation. In table 13 the numbers of cocoons are expressed in terms of the average for three meter quadrats and five felled trees.

The numbers of cocoons per unit area of ground vegetation vary greatly with the size of the caterpillar population, the degree of defoliation, and the amount of caterpillar wandering. In areas having been completely defoliated the number of cocoons varied from 97.6 to 17.5 per square meter. When expressed as cocoons per acre the numbers would be approximately 400,000 and 75,000, respectively. In one area in which a spraying experiment was conducted the average number of cocoons per cubic quarter mile acre for the sprayed plot was 0.3 as compared to 27.79 for the unsprayed area. When calculated on an acre basis the numbers would be 1,200 and 111,160, respectively. The greatest concentration of cocoons encountered in this study was 682 which were spun in a clump of red maple sprouts with a volume of about two cubic meters. Few large trees were cut to obtain information regarding the density of cocoons when there was partial defoliation of the crowns. One 4-inch tree with about

Table 13. Cocoon Numbers in Seven Sample Plots Studied Near Itasca State Park

Plot Number	History of Defoliation	Cocoons per Square Meter	Cocoons per Tree
1	None	0	0.7
2	Complete 2 years	55.0	0
3	Complete 2 years	62.0	0
4	Complete 1 year	46.3	0
5	Medium 1 year	4.3	27.7
6	Complete 1 year	54.0	0
7	Light 1 year	0.3	6.2

75 per cent defoliation had 676 cocoons. The labor involved in making such counts reduced the number of attempts.

Some information on the relation between the number of moths emerging per tree and the number of eggs deposited in the same area is available from observations made in the plots listed in table 13. The cocoon samples were taken after the period of moth emergence, and so it was possible to determine the average number of moths which emerged per tree. The openings in cocoons from which moths have emerged are easily recognized by a characteristic stained aperture. When the number of moths per tree is known, this value when multiplied by the sex ratio of about .5 will give the approximate number of eggs which could be found in each tree. The calculated and actual number of egg masses per tree is presented in table 14. The differences shown are quite significant when one considers the characteristics of the plots and their defoliation history. Plots 2 and 3 listed in tables 13 and 14 were composed of 4- and 5-inch trees and were poorly stocked with only 370 and 490 trees per acre, respectively. They had both been completely defoliated for two years so that there had been time for over-population to occur. There is circumstantial evidence that many of the moths moved out of the area into neighboring stands which were not badly infested. Plot 7 was a few hundred yards south of plots 2 and 3 and showed a greater number of eggs than could have been deposited by the moths which were produced there. Plots 4 and 5 were well-stocked stands of trees about 2 to 3 inches D. B. H. The calculated and actual numbers of eggs show a remarkable agreement. The lack of moth movement may have been due to the not too dense population and the small size of the trees. It is possible that tall trees such as those in plots 2 and 3 bring about migration indirectly. The moths fly up into the crowns 50 feet or more high and may be carried away by the wind more easily. It can be seen that any estimation of the probable number of egg masses based upon cocoon samples must be made with discretion.

Table 14. The Estimated Number of Egg Masses Per Tree Calculated From Unit Area Cocoon Counts

Plot Number	Calculated Number Egg Masses per Tree	Average Number of Egg Bands in Felled Trees
2	115.1	75.4
3	91.0	61.6
4	15.5	17.1
5	14.8	15.3
7	3.5	16.3

NATURAL CONTROL OF *Malacosoma disstria*

There are species of noxious insects against which methods of applied control are used very little or not at all. Most of these insects are forest species which are not perennial pests but instead they appear in outbreak numbers only at irregular intervals. The standard remedies which are successful in the control of orchard and garden insects are not used for them extensively either because of the large areas infested, the comparatively low value of some forest crops, or technical difficulties associated with control operations. One of these insects, the forest tent caterpillar, is easily controlled by spraying with arsenate of lead only in orchards, parks, and around resorts where the spraying operation is economically feasible. When the caterpillars are present in destructive numbers in the forest, the usual procedure has been to let nature take its course. Nature has responded by terminating most outbreaks in from three to five years. One of the final purposes of this investigation was an analysis of the working and importance of natural control factors which terminated the recent outbreak of *Malacosoma disstria*. The following discussion will include field observations on the effects of the various elements of weather and of natural enemies on populations of the forest tent caterpillar.

Mortality During the Egg Stage

The eggs of the forest tent caterpillar are deposited during the first week in July and embryonic development is completed about three weeks later. During this rather brief period the species is subject to the first of a sequence of encounters with environmental factors which reduce the numbers. The first egg mortality occurs soon after oviposition as shown by Hodson (5). In this study of egg parasitism, it was shown that the parasites are active during the period of moth flight. As shown in table 9 the number of eggs destroyed by parasites is rather small, averaging 2.2, 7.2, and 7.8 per cent for 1936, 1937, and 1938, respectively. That the surprisingly low rate of parasitism is due to parasite inefficiency was also suggested in the paper mentioned above. For example, in 1937 the percentage of individual eggs parasitized was 7.2, and yet the average number of egg bands attacked was 73.1 per cent. It was concluded that at least three parasite species were well adapted to the life cycle of the host, but factors associated with oviposition and egg mass construction brought about the low rate of parasitism. The value of egg parasites as a natural control agent cannot, however, be measured entirely by the small fraction of the population which they destroy. This small fraction sometimes is all that is necessary to bring the pest under control when added to the numbers acted upon by other control factors.

Saunders (15) attributed much importance to mites of the genus Trombidium which were thought to feed on the eggs of the forest tent caterpillar. Mites were also present under the egg bands of a high percentage of the samples studied in this investigation, but there was absolutely no evidence that they were attacking the eggs or larvae. In some masses of eggs in which all the enclosed larvae were living there were hundreds of mites resting on the under sides of the eggs. Probably they took advantage of the shelter afforded by the bands and merely passed through the winter under them.

In table 9 there are columns of figures headed with the expression "dead eggs." These were eggs in which there had been no embryonic development or eggs in which no larvae were formed. Usually there was no evidence of any embryonic development, and the eggs had the appearance of the yolk of a hard-boiled egg. The data show that the percentage of dead eggs was remarkably greater in 1936 than in 1937 or 1938, in fact the lowest percentage in 1936 exceeded the highest in 1937. Fortunately, the circumstances prevailing at the time of egg deposition in 1936 and 1937 are known, and they afford a reasonable explanation for these highly significant differences. During the first two weeks in July, 1936, there was a record-breaking heat wave in Minnesota. Temperatures reached as high as 107° F. even in the forested, northern part of the state, and there were several consecutive days on which the temperature rose above 100° F. Associated with the extremely high temperatures was an unprecedented drouth. This period of unusual weather coincided exactly with the period of maximum moth flight and egg-laying. The intensity and duration of the heat varied throughout the area infested by the forest tent caterpillar. In the western edge of the area there were as many as nine days with a maximum temperature over 100° F. and an absolute maximum of 107° F. In the central part of the area there were three or four days with a temperature of 100° F. or over and the absolute maximum was 102° F. Along the shore of Lake Superior the temperatures were unusually high, but they did not rise above 100° F. In general, the rate of egg mortality corresponded with the differences in heat, with a few exceptions. Factors other than the maximum temperatures reported by weather stations explain the irregularities in mortality records. First, the location of instrument shelters is of great importance, and the sites selected may or may not represent average conditions of the surrounding area. Secondly, the location of the stand with respect to exposure and air currents and the size of the trees are also important factors. In one locality, eggs in trees 50 feet tall showed a mortality of about 25 per cent, while across a trail 55 per cent of the eggs in trees 15 feet high were killed. Rangers reported a similar condition in several other localities.

In one area, in which the caterpillars were abundant during only one year of this study, the mortality was very high. Five samples of eggs collected near Detroit Lakes and Perham, Minnesota, showed the following percentages of undeveloped eggs: 89.6, 92.8, 91.5, 90.6, and 93.4. These localities are nearly on the edge of the prairie where there were nine days during the egg-laying period when the temperature rose to 100° F. or above and a few miles west of them a maximum temperature of 114° F. was recorded.

In 1937 and 1938 the temperature was much more moderate during the period of mating and oviposition. The maximum temperature reported by any of the weather stations in the infested area was 97° F., and there was considerably less injury to the eggs. There is no way of determining whether the failure of the so-called "dead eggs" to undergo cleavage was due to partial infertility of the females or to injury after the eggs were laid. Other studies, such as those of Oosthuizen (11), indicate that high temperatures may interfere with successful mating and usually cause a decrease in both fecundity and fertility of injured females. In this case there was no reduction in egg mass size in localities where the highest mortality was observed, and it may be that there was a greater injury to the deposited eggs than to the parent moths.

Table 9 also shows that there was little mortality among larvae in diapause in any year. The death rate was slightly higher in 1936 than in the other years and may have been caused by some injury to those eggs which were not killed by the July heat. This possibility is also suggested by observations made on egg masses collected from the area in which there was such a high mortality. In some cases the number of dead eggs was small, but in nearly all such masses the number of dead larvae was unusually large.

The prediction of caterpillar abundance was based largely upon samples of egg bands collected during the fall and early winter. Possibility of winter mortality was considered in making the fall collections. However, little winterkill was observed in spite of the low temperatures. In the winter of 1935-36 temperatures as low as —52° F. were recorded in areas populated by the forest tent caterpillar, and severe cold weather persisted longer than had ever been reported before in the state. There were several days with temperatures below —30° F. and weeks with temperatures below 0° F. Egg masses were collected in the spring to be compared with data prepared from samples taken the previous fall. There was no significant difference in the mortality figures. In fact, the average larval mortality was slightly less in the spring. This condition was, of course, due to errors of sampling rather than revival. Laboratory tests also show that the over-wintering larvae can endure very low temperatures without freezing. However, it is only during the dormant period that the cold-resistance is so marked.

In March, 1938, another unusual weather condition was reported. The average temperature was much higher than had been reported before, and the average maximum temperature was more than 10 degrees above those recorded for other years during the outbreak. A maximum of 71° F. was recorded about the middle of the month. This unusually warm temperature activated some of the hibernating forest tent caterpillar larvae to the point where some of them even started to chew through the egg shells. Following the period of unseasonable temperature there were several days when the minimum temperature dropped to about 0° F., and temperatures below 0° F. were reported in early April. Laboratory experiments performed in this investigation and laboratory studies mentioned by Salt (14) indicate that although the unhatched larvae are very cold-resistant, upon hatching, 100 per cent may be killed by very short exposures to temperatures a little above 0° F. Egg samples were taken in May, 1938, after the hatching period to observe the effect of the March weather conditions. When compared with the mortality records assembled from samples taken the previous fall a striking difference is evident. The total mortality in the fall, including the number of dead eggs, parasitized eggs, and dead larvae, averaged 15.89 per cent for all the study areas. In the spring the average mortality increased to 60.9 per cent as the direct result of the kill during March. The latter figure represents average conditions in all but the localities near Lake Superior where temperatures were not high enough in March to cause any premature larval activity and so the larval mortality remained low.

Mortality Among Feeding Larvae

Unless feeding caterpillars are studied under insectary conditions or are studied very intensively in the field, it is often difficult to obtain good data concerning the causes of mortality. In this investigation the observations are rather meager. They give some idea of some of the factors involved without providing a basis for their complete interpretation.

The direct action of physical environmental factors is often the cause of high mortality, particularly among first instar individuals. During two of the years in which a rather intensive study was made of forest tent caterpillar populations there was little evidence of mortality among the small larvae. However, in the spring of 1938 a high mortality could be attributed to unfavorable weather. In late April and early May the temperatures were high and stimulated hatching which began about May 5. This year the hatching was completed before many buds were beginning to burst, and soon afterward there was a period of cold weather which lasted for about three weeks with little interruption. During this period the temperature fell below freezing several nights and unusually heavy rains occurred. The leaves opened very slowly, in some localities there was no foliage for the caterpillars for over two weeks after they had hatched, and in addition the small leaves were frozen in many places. The tiny larvae remained clustered on or near the mass of eggs from which they emerged, and in many cases there was a mortality of 100 per cent. From May 17 to 29, 25 trees in several infested areas were examined to determine the death rate among these hatched larvae. When the number of larvae present on the trees was compared with the number which had hatched from egg masses on those trees there was an average survival of only 11.7 per cent with a range of from 0 to 36 per cent. The combined action of rain, wind, freezing temperatures, and the absence of food caused large losses, again with the exception of some localities near Lake Superior. In this region the weather conditions were not favorable for hatching until late in May and afterward remained suitable for normal development.

There is little evidence that weather conditions cause much mortality after the second instar. However, there were a number of other factors of more or less importance. Caterpillars were attacked in the third instar by an undetermined species of parasite. This species was not very successful, at least in the area around Itasca State Park. Other natural enemies cause some mortality among the feeding larvae, but there is no information available concerning the actual amount of good they do. The following insects were seen feeding upon caterpillars: *Podisus placidus* Uhl., *Calosoma calidum* Fab., *C. frigidum* Kby., and an undetermined Carabid larva, probably *Calosoma* sp. In some insectary studies, adults of *Calosoma frigidum* ate or destroyed an average of 2.7 caterpillars per beetle per day, and fed at this rate for more than two weeks. Some of the killing was caused more by savagery rather than hunger.

Some notes on the life cycle of this species were taken as purely incidental observations. Eggs laid on June 17 hatched on June 23. The third instar, which is the last, was started on June 29, and pupation occurred on July 26. Pupation was accomplished in about 11 days. Several adults were left without food and lived for more than a month under conditions of complete starvation. These beetles were often seen on the ground and also up in the crowns of trees infested by the forest tent caterpillar. There is no way of estimating their true value, but they must have contributed something to the general population decline.

Birds may have fed on the small larvae, but in spite of repeated attempts to watch the process no birds were observed in the act. Wilt disease was another element of natural control which has been reported as a very important factor, but in Minnesota its importance was not very great. Wilted caterpillars were not uncommon in areas visited near Itasca State Park, but they were estimated to be less than one per cent of the population. In 1936 numerous wilted caterpillars were reported near Ely, but no actual counts were made. Species of Tachinids also attack the older larvae, those in the late fourth and fifth instars. Their success is so closely related to the action of another parasite that they will be considered in the next section.

Mortality of Prepupae and Pupae in the Cocoon

Several thousand cocoons were collected over the entire infested area to obtain information concerning the environmental factors which might be causing further mortality after the feeding period. Although extensive collections were made only during the summer of 1937, there are some quite complete records of

Table 15. Total Parasitism of Prepupae and Pupae in the Cocoon in Per Cent for Several Localities in Northern Minnesota, 1936-1938

Locality Number	Percentage of Parasitism		
	1936	1937	1938
1	80.8	....	....
2	85.5	85.6	99.6
3	....	91.0	99.2
4	....	95.6	99.3
5	....	91.0	No cocoons
6	70.9	90.6	....
7	72.7	87.2	No cocoons
8	62.0	81.3	No cocoons
11	....	74.5	99.7
12	....	76.7	No cocoons
14	....	50.7	....
17	58.6	75.9	98.4
18	40.5	71.2	99.8

parasitism for a few areas. The percentage of parasitism during 1936 through 1938 is shown in table 15. The localities are numbered according to the numbers and locality descriptions given in table 8.

The tabulated data show definitely that parasites played an important role in preventing an unrestricted increase in the caterpillar population. Except in Locality No. 2, there was a progressive increase in parasite efficiency as time elapsed. In the second, third, and fourth localities, the cocoons were collected in stands where there had been complete defoliation in 1938. In the other three areas where cocoons were found in 1938 the population had been decimated earlier in the season, and the parasite data were collected from small numbers which survived. In some areas no cocoons were found by the field men but that could mean only that scattered cocoons present in the crowns were overlooked. In some stands examined near Itasca State Park there was an average of less than one cocoon per tree even in trees 4 inches or more D. B. H.

The parasites responsible for the heavy parasitism indicated in table 15 were not determined to species in many of the collections made. The cocoons were taken after the period of moth emergence at a time when most of the parasites had also emerged. Nevertheless, it was possible to distinguish the unmistakable signs of the former presence of certain particular species and in other cases the family. In numerous cases samples were collected at various times previous to the first moth or parasite emergence, and the parasites were reared from these collections of cocoons. The species of parasites include *Sarcophaga aldrichi*

Parker, *Itoplectis conquisitor* (Say), at least two species of Tachinids, and a small undetermined hymenopteron which seemed to exhibit polyembryony. The first species, *Sarcophaga aldrichi,* so dominated the picture that the other species appeared inconspicuous in comparison. As demonstrated by Hodson (6), *S. aldrichi* is a scavenger and a very active and extremely effective parasite of the forest tent caterpillar. It was present in very large numbers throughout the entire infested area, and it was responsible for about 97 per cent of the total parasitism. It exhibited a very significant intrinsic superiority over other competing species. Tachinids which attacked the fourth and fifth instar larvae were destroyed by the Sarcophagid maggots which enter the same hosts after cocoon formation. Likewise, the larvae of *Itoplectis conquisitor* were killed indirectly by the feeding activity of *S. aldrichi.* In many samples, 100 per cent of the successful parasites were maggots of this species. The adult fly is a strong flier, and it was observed often several miles from the nearest area infested by the host.

Table 15 shows that the percentage of parasites present in the various localities varied with respect to the number of years in which there had been a large caterpillar population. In most areas under observation the parasitism approached 90 per cent during the third year of heavy defoliation, but under some conditions a high percentage of parasite attacks was observed earlier. In one locality near Ely, Minnesota, the cocoon parasitism was 50.7, 70.9, and 90.6 in 1935, 1936, and 1937, respectively, definitely increasing each year. No cocoons were collected in 1938 because the population had been reduced to a very low level. In this particular area the first complete defoliation took place in 1934.

Three experimental plots located north of Itasca State Park also showed an increase in the parasite population as the outbreak persisted. These plots were completely defoliated first in 1936 when the average parasitism was 40.5 per cent. The next year parasitism on the same plots increased to 71.2 per cent. In 1938 there were very few cocoons found in this area, but every one found had been successfully attacked by *Sarcophaga aldrichi.*

In 1936 a study was made of parasitism in areas with a very dense population of caterpillars and cocoons, and the results compared with nearby stands with varied populations. Cocoons were sampled at half mile intervals from a point near the center of a localized outbreak to another point two and one half miles farther south where there were very few, widely scattered larvae.

The results from collections of about 300 cocoons taken at each station are as follows: 41.3, 47.8, 61.9, 72.4, and 89.1. These figures indicate that the population surrounding the area with complete defoliation was being heavily attacked, probably by parasites which spread out from the area of great host concentration. Most of the parasitism in the outlying forest was caused by *Sarcophaga aldrichi* which ranges far from the center of population.

A similar difference in the percentage of parasitism was observed in three permanent sample plots. In one there was complete defoliation and 54 cocoons per square meter; another was partly defoliated and had 4 cocoons in the quadrats; a third showed only slight defoliation and 0.3 cocoons per square meter. The cocoon parasitism found in each of these plots was 70.4, 80.3, and 87.9 per cent, respectively. The condition described may help explain one common observation. Complete defoliation usually occurred in rather sharply defined areas with little damage in stands of trees nearby. In addition, new infestations usually were caused by the movement of larvae or moths from neighboring areas instead of developing independently. Such a procedure may be caused partly by the suppression of small populations by parasite migration. Parasites can increase rapidly where there is abundant host material and then extend their range into areas where the scarcity of larvae would otherwise restrict their numbers.

One unique although unimportant incident was observed during the summer of 1937. The author and an assistant noticed thousands of cocoons littering a woods trail for about 400 yards. These cocoons were all opened and were distributed quite constantly in small groups. As the observers approached a large flock of crows flew away. Their tracks were present in the road dust around each of the collections of cocoons. The area was watched for several minutes from a clump of hazel brush which hid the observers from the crows. They returned soon and proceeded to tear cocoons from their place of attachment, carry them to the road, open them by holding them down with their feet, and devour the contents. Cocoon counts had been made in this particular stand of timber a few days before. A second count was made the day after the crows were observed, and they had reduced the number of cocoons about 20 per cent. They probably did more harm than good because about 80 per cent of the larvae and pupae were parasitized, and the crows did not select the unparasitized individuals.

Adult Mortality

It was practically impossible to determine the fate of moths after they had emerged and were in flight. Large numbers died without depositing any eggs, but the percentage of the population involved could not be even estimated. While flying, large numbers of moths were attracted to town and city lights and were destroyed, and thousands fell in large lakes and drifted onto the shores. In some cases these losses may have had a very significant effect upon the local population, but they cannot be evaluated.

When cocoons were collected after moth emergence, the number of dead moths left behind could be easily determined. In most of the areas these numbers represented a very small proportion of the population. However, in 1936 the unusual heat in July caused a very heavy moth mortality in the extreme western portion of the infestation. Cocoons collected in the areas where there was a high egg mortality contained dead moths which made up 19.6 per cent of the total population and 42.8 per cent of the moths. In these same localities, selected near Detroit Lakes and Perham, the parasites also suffered from the heat with 92.6 per cent of the dipterous and hymenopterous parasites being killed. Farther east the dead moths were less prevalent; they constituted an average of 3.2 per cent of the total population and 11.9 per cent of the moths which developed. In 1937 the number of moths which died before they could escape from their cocoons was uniformly low and was of little importance. The number which died represented only 1.2 per cent of the total population or 4.9 per cent of the fraction of the population which had become adults. In 1938 the corresponding values from the few areas where cocoons were collected were 0.4 and 13.3. The percentage of the total moths which were dead varied from 0 to 50 per cent because in some cases where there was only one dead moth there was also only one live moth which had emerged from the sample of cocoons.

An Evaluation of Mortality Factors

These records of mortality provide information for evaluating the regulatory action of environmental factors. The figures obtained from the rather extensive field observations represent only minimum values because there are additional deaths in the population which have escaped attention. The most detailed obser-

Table 16. Environmental Factors Responsible for Mortality in All Stages of the Forest Tent Caterpillar as Observed near Itasca State Park, 1936-1938

Stage of Development	Mortality Factor	Apparent Mortality in Per Cent			Real Mortality in Per Cent		
		1936	1937	1938	1936	1937	1938
Egg	Parasites	2.2	7.2	7.8	2.2	7.2	7.8
	Weather and possible infertility	32.9	8.6	19.9	32.9	8.6	19.9
Larvae in diapause	Weather probable factor in 1938	5.1	0.9	46.2	3.3	0.8	33.4
Feeding larvae	Weather	......	......	86.9	......	......	33.8
Prepupae and pupae in cocoons	Parasites	40.5	71.2	99.8	24.9	59.4	5.0
Adults	Weather	3.4	1.8	0.0	1.2	0.3	0
Total mortality	Weather	......	......	......	37.4	9.7	87.1
Total mortality	Parasites	......	......	......	27.1	66.6	12.8
Grand total		......	......	......	64.5	76.3	99.9

vations were made near Itasca State Park, and the known causes of mortality over a three-year period in this area are listed in table 16. In the following discussion it will be noted that in some details the specific causes of mortality vary from one locality to another as one might expect from results obtained in other similar studies, and, furthermore, the causes of mortality in one locality differ from one year to another.

The data presented in table 16 represent the average mortality caused by a number of environmental factors. The percentages of mortality are expressed as *real* or *apparent*, terms used by Thompson (18) to distinguish between the percentage of surviving fractions destroyed by any agency and the percentage of the total population destroyed by the same factor. In the tabulations given the apparent and real mortality are the same for two factors affecting the eggs which lie at the beginning of the developmental series. It is assumed that this treatment of the observed mortality is correct because there was no evidence that parasites selected the undeveloped eggs.

Before any comparison is made between the control value of environmental factors it is necessary to consider the mortality which is required to keep the population at a constant level. When the reproductive potential is an average of 150 eggs per female, 98.7 per cent of the progeny of one pair must be destroyed in order to bring the number of surviving adults back to the level of the parent population, and 99.3 per cent must be eliminated to reduce the population to one half of its original size. When the egg masses are smaller or larger than 150 eggs per band, the coefficient of destruction will be decreased or increased accordingly. During 1936 and 1937 the total mortality fell far below the amount required to check population increase, while in 1938 the population was almost completely destroyed. When the per cent mortality for each of the three years is expressed in terms of the number of moths which would survive from an initial number of 150 eggs, there would be 53.3, 35.8, and 0.2 for 1936, 1937, and 1938, respectively. The spring frost caused a very high mortality, probably of more importance than the figures indicate. However, the percentage of parasitism as observed after the cocoons were spun was high enough to nearly wipe out the caterpillars without other mortality. One might be led to believe that the parasites were of more value than other factors if one important fact is not considered. Although the cocoon parasitism was 99.8 per cent, it represented a real mortality of only 5 per cent. There is no way of determining what the parasite efficiency would have been if the population had not been reduced greatly before the larval and pupal parasites had a chance to attack. These parasites, however, performed a valuable service by destroying a small fraction of the population which might otherwise have been sufficient to cause damage.

Thompson (19) stated, after making a careful study of the natural control of the European corn borer, *Pyrausta nubilalis,* that population regulation was produced by a complex group of factors and that no one factor was demonstrably capable of controlling the corn borer in the absence of others. There is further evidence from the present investigation that most of Thompson's conclusions apply equally well to the forest tent caterpillar. The data for Itasca State Park have shown that the outbreak in that locality was terminated by a combination of many factors, with late frost and parasites playing the dominant role. Two other areas show to what extent there may be differences in the specific causes of death. These are Perham, in the western edge of the infestation, and Grand Marais on the eastern margin. There are no observations concerning the mortality among feeding larvae for either of these localities, but it could not have been very significant in either case because complete defoliation and extensive caterpillar movement took place during the last years of the outbreak. The controlling factors responsible for the termination of the outbreak in Perham, 1936, and Grand Marais, 1938, are given in table 17.

In these two areas conditions were quite different from those in Itasca State Park, and they varied one from the other. At Perham the prepupal and pupal parasites were not very numerous, and the high temperatures during July were much more significant. Yet, the parasites contributed much toward the

Table 17. Environmental Factors Responsible for Mortality in All Stages of the Forest Tent Caterpillar Observed During the Final Year of the Outbreaks in Perham and Grand Marais, Minnesota

Stage of Development	Mortality Factor	Perham, 1936		Grand Marais, 1938	
		Apparent mortality	Real mortality	Apparent mortality	Real mortality
Eggs*	Parasites (4)	1.4	0.1	5.7	5.7
	Weather (3)	89.1	23.1	8.6	8.6
Larvae in diapause	Weather (5)	6.6	1.8	0.1	<0.1
Prepupae and pupae in cocoons	Parasites (1)	53.5	53.5	99.4	85.1
Adults	Weather (2)	42.8	19.6	0.9	<0.1
Total mortality	Weather	....	45.5	....	8.6
Total mortality	Parasites	....	53.6	....	90.8
Grand total		....	99.1	....	99.4

* Egg samples taken during the spring of 1937 in Perham and the mortality sequence is indicated by numbers in parentheses. In Grand Marais the egg mortality was observed in the fall of 1937 and the sequence is the same as in table 16.

eventual near eradication of the forest tent caterpillar. Probably the real mortality caused by heat would have been higher than indicated if the parasites had not previously depleted the population, because, like other physical factors, high temperature operates as a density independent factor. It is probable that the possible value of a controlling factor is often masked by the action of another. For example, fifth instar caterpillars collected at Itasca State Park in 1938 showed a parasitism of 97.1 per cent caused by a tachinid, *Zenillia protuberans* A. and W., and yet all of the cocoons collected in the same locality produced the maggot of *Sarcophaga aldrichi.*

In the locality inland from Grand Marais the parasites, mostly *Sarcophaga aldrichi,* were chiefly responsible for a tremendous population reduction which was not preceded by a decimation of the caterpillars by other factors, such as freezing temperatures. It seems probable that these parasites might have been successful in other localities farther west, but a more complex sequence of events prevented an answer to the question.

The mortality data presented probably do not agree in all particulars with the exact conditions in the field; i.e. there are mortality factors left unaccounted for in the description of the events. However, it is unlikely that they err in being too high and are, therefore, on the safe side. In general the results confirm the basic conclusions of Thompson (18) who made the following statement: "The real significance of a controlling factor depends, however, not merely upon the fraction of the total host population it actually destroys, but rather upon the fraction of population for the destruction of which it is indispensable."

Table 18. Years of Outbreaks of *Malacosoma disstria* in North America, 1886 to 1940

	Maine	New Hampshire	Vermont	Massachusetts	New York	Connecticut	New Jersey	Virginia	South Carolina	Mississippi	Louisiana	Pennsylvania	Michigan	Minnesota	North Dakota	Montana	Washington	Oregon	California	Colorado	Eastern Canada	Central Canada	Western Canada
1886			x																				
1887	x	x	x	x	x	x	x														x	x	
1888	x	x	x	x																	x		
1889	x	x	x																		x		
1890	o				o												x				o		
1891									o					x	x		x	x					x
1892																	x	x					x
1893																	x	x					x
1894																		x					x
1895			o																				
1896		o	x	o	o																		
1897	x	x	x	x	x																x		o
1898	x	x	x	x	x								x	x			x				x		x
1899	x	x	x	x	x																x		o
1900	o		o		o																o		
1901																							
1902																						o	
1903																							
1904																						x	
1905																							
1906																							
1907																	o						o
1908																	x						x
1909	o																x						x
1910	x																x				x		x
1911	x	x	x	x										x			x				x		x
1912	x	x	x	x										x			o				x		o
1913	x	x	x	x																	x		
1914	o	o	o	o																	o		
1915																	o						
1916																							
1917																							
1918																							
1919														x									x
1920														x									x
1921														x				x					x
1922	x			x										x	x								
1923	x			x	o	x	o							o	o			x			x		
1924	x				x		x											o			x	x	x
1925																						x	
1926													x									x	
1927				o															x			x	
1928																	o					o	
1929														o			x					o	o
1930				o				x						o			o		o				
1931	x							x			x						o						
1932	x							x														x	
1933	x	x	o					x			x	x		x						x	x	x	
1934	x	x	o			o				x				x						x	x	x	
1935	x	x	x	x	x	x				x	o	o	o	x						o	o	x	x
1936	x	x	x	x	x	x	o		o	o	x		x	x		x	o					x	x
1937	x	x	x	x	x	o			x			x	x	x								x	x
1938		o	x	o	x	o			x	x		o	x	o	o		x	o				o	
1939			o		x	o	o					x	x		o	o	x	o				o	
1940			o	o	x	o				o		x	o					o		x			

x = General outbreak o = Local outbreak

THE CYCLIC BEHAVIOR OF POPULATIONS OF *Malacosoma disstria*

Among the introductory remarks, it was suggested that population gradations have occurred at about ten-year intervals and have taken place in widely separated parts of North America at nearly the same time. Outbreaks which have been reported since 1886 are tabulated in table 18. The occurrence of these major disturbances is well established, but the exact date of the beginning and the duration of many of the earlier outbreaks cannot be determined.

Although outbreaks were known earlier than 1886, records previous to this date were less complete and weather reports contained much less detailed information. The occurrence of these periodic fluctuations has aroused considerable interest and some speculation concerning possible causes, though most published comments have been general discussions of natural control or occasional reports on the action of some one controlling factor. Recently Sweetman (17) has reviewed some of the opinions reported in the literature and has concluded that spring weather is probably the most important check for both *Malacosoma disstria* and *M. americana.* The paper is not as convincing as it might have been if the author had shown a greater familiarity with the actual sequence of events which take place during an outbreak, and he has dismissed some factors such as larval and pupal parasites without adequate treatment. Spring frosts are regarded as the most important ecological factor, and yet only one of the references quoted is supported by counts, that one dealing with the destruction of the eastern tent caterpillar. Furthermore, papers giving concrete evidence of heavy parasitism have been omitted; among these are contributions from Caesar (3), Hodson (6), and several reports in the Insect Pest Survey Bulletin, as well as other accounts of heavy parasitism such as that of Brown (2).

Our knowledge concerning the real environmental complex responsible for the termination of outbreaks is very limited because most of the observations reported are either qualitative or limited to one of a probable sequence of factors. The present study demonstrates that even in a single state as many as three major environmental factors may play a dominant role in different localities. Although there is much too little good evidence available to describe the conditions during the year or years when many outbreaks have subsided, many contributing factors of natural control are known. These are: spring frosts, high summer temperature, parasites, disease, and starvation.

Following many of the reported outbreaks there has been an extremely low population. How few caterpillars may be present is illustrated by the results of repeated searchings made in 15 study plots and in additional areas near Itasca State Park. In two years one caterpillar has been found, that one during the second year after the general population decline. The importance of this extremely low population level is readily understood when one considers its relation to the subsequent growth of another large population.

Let us consider the time required for the unrestricted development of a population which can completely defoliate a stand of aspen having about 1,000 stems per acre and falling in a common diameter class of 4 inches D. B. H. If we assume that there is one pair of moths present in areas of 1, 5, or 10 acres, a reproductive potential of 150 eggs per female and a sex ratio of .5, the time necessary before complete defoliation could occur would be four years for the highest density and five years for densities of one pair in 5 or 10 acres. After the population has started on its geometric progression, the rate of increase is very great as shown by the fact that with one pair of moths in about 50 acres six years would be required as compared with five years when there is one pair in 5 acres. The delay in repopulation of areas is undoubtedly increased by the action of several elements of natural control.

As shown in table 18 the period of time between outbreaks varies from about 7 to 11 years. It is possible that natural catastrophes may interrupt the progress of a population more than once during its ascent, and produce the recorded differences in intervals of time. It is unlikely that anyone will be able to determine the actual numbers of moths present at very low densities. However, some intensive studies are planned to observe the facts associated with population increase. It is usually assumed that the development of large populations takes place rapidly when some environmental pressure is removed, but the delay commonly observed may be greatly influenced by the size of the initial population.

The characteristic of the fluctuating populations of *Malacosoma disstria* which is most difficult to explain is the appearance of extensive defoliated areas in nearly all parts of the United States and Canada at about the same time. One suggestion which has been given some study has been the occurrence of periods of particularly favorable weather which may have been common to the entire country. A careful investigation of weather conditions existing during the critical periods in the life history of the host failed to show any consistent agreement. It is unlikely that the same conditions would be found simultaneously in such widely separated regions as South Carolina, Louisiana, Washington, Minnesota, New England, and the Canadian provinces; and furthermore, records of average maximum, minimum, or mean temperature and total rainfall would not provide the needed information. A few days or possibly hours when the insects were exposed to extreme conditions might be sufficient to cause a high mortality. Daily weather records from several points in Minnesota over a number of years indicate that during the two or three years prior to the first complete defoliation there are fewer days when the temperature falls below freezing after the usual hatching time; but, unfortunately, the control exerted by cold and rain cannot be evaluated with certainty because before 1936 there is no information concerning the exact time when the first instar caterpillars appeared. The complexity of the problem, as illustrated by the events described for the last outbreak in Minnesota, is such that no simple formula or generalization will produce the answer.

The manner in which the infestation spread over much of northern Minnesota was described earlier. There were a few separate centers from which the population spread rapidly over a wide area. Furthermore, even though there were differences of from two to five years during which there was complete defoliation, the outbreak subsided over the entire area about the same time. These observations may throw some light on the question of parallel population gradations. It seems logical that the greatest rate of dispersal of the species would take place during times when there were high concentrations of moths. Moths would fly or be blown into nearby areas with low populations or where the pest was not present, and the result would be a considerable extension of the infested area. After the process was repeated two or three seasons there could be a rather large area involved. Then either some inclement weather condition, disease, or the increase of natural enemies would terminate the outbreak over the original area and all invaded localities. Such a population drop takes place from three to five years after the first heavy defoliation. It is likely that the numbers of survivors per acre would not be exactly the same over the entire area. There would be scattered islands with a few individuals and other localities where the insect was completely exterminated. Finally, after the required time had elapsed, the caterpillars would again become abundant, but instead of one center with a concentrated population as before there would be a variable number of loci from which a more severe outbreak could develop. These several localities with complete defoliation would be observed at about the same time because they had previously subsided in the same year. In this way outbreaks isolated from each other by uninfested or lightly infested areas could occur simultaneously. In Minnesota there was a difference of two or three years in the time when individual, widely separated areas were damaged badly and, with the exception of one area, the caterpillars disappeared during the same season over a large area. Even though there were differences of one or two years in the initial appearance of hordes of caterpillars the coincident termination of the outbreak would tend to keep the fluctuations in separated areas nearly parallel. Such a process could take place in one state or even in a comparatively uniform area such as New England, but country-wide population fluctuations cannot be explained by this means. Table 18 indicates that there are irregularities, which are due probably to regional conditions, that have changed the population dynamics and have thrown them out of phase with other areas.

If the forest tent caterpillar continues to exhibit the periodic fluctuations which have occurred before, there should be another series of outbreaks beginning in about 1945 in many parts of the country. The increasing severity of these outbreaks which has been observed in Minnesota and has also been reported for Canada by Tothill (20) and Brown (2) is probably caused by the very great increase in aspen, one of the favorite host trees. This species has replaced coniferous trees which have been removed by logging and fire and at present is distributed in almost continuous stands over large areas in most of the northern forests (Kittredge and Gevorkiantz [7]). As a result the spread of the forest tent caterpillar has been greatly facilitated and the difficulty of control increased. Further study may show that the suppression of initial centers of dispersal will prevent the general devastations caused by the caterpillars.

Finally, it is evident that for a complete understanding of population fluctuations in one restricted locality or of the more fascinating simultaneous appearance of the species over very large areas, we must have more intensive observations and more quantitative data accumulated during future outbreaks.

SUMMARY AND CONCLUSIONS

1. The history of outbreaks of the forest tent caterpillar, *Malacosoma disstria,* in the United States and Canada is reviewed with particular reference to reports since 1917. Minnesota records are discussed and the history of the most recent outbreak described in more detail.

2. The life history of the insect is presented with particular reference to seasonal activities in Minnesota, the effects of temperature on the rate of development of larvae and pupae, the quantity of food eaten during the period of larval development, and the production of frass. The possibility of using frass collections in making population studies is suggested.

3. A brief study of the host selection and favorable host species is described, and an investigation of the importance of starvation is also presented. It was found that no larvae were able to pupate when they were without food during the last instar, but caterpillars which were allowed to feed for less than one half of the usual feeding time were able to develop into adults. Such mature females contained an average of 97 eggs while the controls contained an average of 172 eggs. This reduction in the number of eggs agreed well with the reduction observed in the field where there had been starvation.

4. Various methods of obtaining population measurements are described. These methods include procedures for estimating the numbers of cocoons, larvae, and eggs. The results of population surveys which were made during 1936-1938 are presented. The most valuable data were secured from the samples of egg bands which could be used as a measure of the total productivity in any area. A method of predicting the probable amount of defoliation to be found the following year is based upon the egg survey and a knowledge of tree characteristics. The use of this method and the steps necessary to obtain the required information are given along with some of the difficulties.

5. The natural control of the forest tent caterpillar in Minnesota is discussed in great detail with special emphasis being placed on the action of various factors in bringing an outbreak to a close. It was found that no single factor was entirely responsible for reduction in numbers. Instead, a complex situation was observed in which several factors acted in sequence, each destroying a fraction of the population in one or more of the

stages of development. In three different parts of the state a different agent of natural control was preeminent. In one area high summer temperature was very important, in another a spring frost after the hatching date was destructive, and in the third area parasites exhibited an unusual degree of efficiency. In all cases there were other contributing factors of more or less importance.

6. The cyclic behavior of populations of *Malacosoma disstria* is examined and some of the possible regulating factors discussed. A theory of the possible origin of parallel fluctuations in numbers in separated localities is presented, and the need for further critical studies on the events which take place during a population gradation is emphasized.

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